Prefrontal-striatal circuitry supports adaptive memory prioritization across development

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Abstract

Previous work has revealed that the ability to strategically encode high-value information may improve gradually over development as cognitive control mechanisms mature. However, studies of value-directed memory have relied on explicit cues of information value, which are rarely present in real-world contexts. Here, using a novel fMRI paradigm, we examined whether individuals across a wide age range (N = 90; ages 8 – 25 years) could learn the value of information from experience and use learned value signals to strategically modulate memory. We found that memory prioritization for high-value information improved across development, and was supported by increased engagement of the caudate and prefrontal cortex during both encoding and retrieval of high-value information. Our results suggest that across development, the dynamic adjustment of memory based on the statistics of the environment is supported by a wide network of brain regions involved in both the recognition and use of information value.

Keywords: **motivated memory; cognitive development; fMRI**

Introduction

In any particular context, all information is not equally useful, and so the value of remembering it similarly varies. A baker who makes bread every day in her pastry shop will likely benefit more from remembering the name of the supplier with the best price on flour relative to the supplier with the best price on tuna. For a sushi chef, prioritizing memory for fish suppliers may be more valuable. Though children may have fewer opportunities to make consequential decisions based on remembered information, they too face many situations in which the need to prioritize memory arises. For example, it may be more useful for a child to remember the television channel that plays her favorite daily show than the the channel that only plays fun cartoons on Saturdays. Indeed, selectively remembering relevant or useful information may be *particularly* beneficial for children, who may encounter more novel information while contending with greater difficulty in forming detailed memories (Ghetti & Bunge, 2012).

Neural mechanisms of motivated memory

Previous research has found that individuals can strategically prioritize memory for information that will enable them to gain more reward in the future (Shohamy & Adcock, 2010), and that this ability improves from childhood to early adulthood (Castel et al., 2011). In young adults, memory prioritization has been shown to involve diverse neural circuitry, including mesolimbic areas associated with dopamine production that have been implicated in reward anticipation, the hippocampus and surrounding medial temporal areas that are critical to memory encoding and retrieval, and the prefrontal cortex (Cohen et al., 2014; Adcock et al., 2006), which may be involved in implementing top-down strategic control processes.

This prior work suggests two possible routes through which value signals may influence memory. First, value signals may elicit dopamine release in the ventral tegmental area, lowering the threshold for long-term potentiation in the hippocampus and other medial temporal lobe (MTL) structures (Adcock et al., 2006). Through this pathway, reward anticipation may directly promote the formation of more robust memories, though the influence of reward anticipation on memory may grow stronger after a period of overnight consolidation (Murty et al., 2017; Patil et al., 2016).

Alternatively, value cues may signal the need for increased control. Through this pathway, value responses in the striatum may trigger the engagement of the prefrontal cortex, which may then influence encoding processes in the MTL, either directly or through other neural systems such as those involved in attentional control Castel et al. (2002). Unlike the direct effects of reward anticipation on memory, those that arise due to the implementation of strategic control may not be consolidation-dependent, and instead emerge immediately.

Despite extensive prior research examining these two mechanistic pathways in adults, to the best of our knowledge, no studies have examined how the functional recruitment of the neural systems that support motivated memory change across development. Whereas the direct influence of reward anticipation and dopamine release on hippocampal memory formation may be age-invariant, the ability to modulate the engagement of control based on value cues emerges gradually over the course of development and, depending on the complexity of the control demands, may continue to improve throughout adolescence as corticostriatal circuitry matures (Davidow et al., 2018; Insel et al., 2017).

Learning value through experience

Past studies of motivated memory processes have relied on explicit value cues at the time of encoding, like dollar signs preceding high-value stimuli. But in the real world, individuals must prioritize memory for useful information in the absence of such explicit cues. To do so, they may extract naturalistic signals of value from the statistics of their environments, and rely on their prior experiences to determine what to prioritize in memory (Anderson & Milson, 1989).

We previously demonstrated that from childhood to adulthood, individuals improve in their abilities to use the statistics of their environment to prioritize memory for valuable information (Nussenbaum et al., 2020). Specifically, we examined whether individuals could use item frequency as a signal of information value. Because many real-world contexts are relatively stable and predictable, the frequency with which one has encountered something in the past often predicts the frequency with which one will encounter it in the future (Anderson & Schooler, 1991), and therefore, the value of remembering information about it. Returning to our previous example, the baker has likely used flour many times in her recent past, so she can infer that she is likely to use flour many times again in her near future. Therefore, she will likely encounter many opportunities in which knowing information related to flour, like its price, can help her make the best purchasing decisions. Similarly, if the child remembers the channel of her favorite weekday show, she will be able to use that information to find it five days each week, whereas remembering the channel of her favorite Saturday cartoon will benefit her on only one day out of seven. We found that from childhood to adulthood, individuals became better both at *learning* the frequency of items in their environments and at *using* that knowledge to prioritize memory for valuable information associated with high-frequency items (Nussenbaum et al., 2020). In our prior work, these effects did not require a period of overnight consolidation to emerge, and instead were present after a brief, 5-minute delay between encoding and retrieval.

The present study

Here, we examined the functional recruitment of the neural circuitry that supports prioritization of valuable information in memory across development. Specifically, we used a task in which individuals first learned the frequency of items in their environments, and then learned information associated with each item. Importantly, we structured our task such that the frequency with which participants first experienced each item indicated the frequency with which they would be asked to report the information associated with each item, and therefore, the number of points they could earn by remembering it. In this way, an item's frequency signaled the value of remembering associated information. Immediately following encoding, we administered a memory test in which participants had to select each item's correct associate. We examined differences in neural activity when participants were asked to encode and retrieve information associated with high- vs. low-frequency items.

Given our task structure — and specifically, the lack of a consolidation period between encoding and retrieval — we expected learned value signals to influence memory through the recruitment of strategic control processes. Specifically, we hypothesized that during encoding, the presentation of pairs involving high- vs. low-frequency items would engage value-responsive regions, including the striatum, and regions involved in implementing strategic control, like the lateral prefrontal cortex (lPFC). Given our previous behavioral findings (Nussenbaum et al., 2020), we further expected younger participants to demonstrate weaker sensitivity to the relative value of high- vs. low-frequency items, reflected in smaller differences in striatal engagement across conditions. In addition, we expected that older participants would show a greater enhancement of lPFC activity during encoding of associations involving high-frequency items, and that this effect would be larger than the age-related modulation of the striatum. Finally, even though participants could only earn one point per retrieval trial, we hypothesized that they would continue to recognize high-frequency items as being associated with greater value, such that they would continue to demonstrate increased striatal responses to high- relative to low-frequency items.

Methods

Participants

Ninety participants between the ages of 8.0 and 25.9 years took part in this experiment. Thirty participants were children between the ages of 8.0 and 12.7 years, thirty participants were adolescents between the ages of 13.0 and 17.7 years, and thirty participants were adults between the ages of 18.32 and 25.9 years. Ten additional participants were tested but excluded from all analyses due to excessive motion during the fMRI scan (n = 8; see exclusion criteria below) or technical errors during data acquisition (n = 2). Participants were right-handed, had normal or corrected-to-normal vision, and no history of diagnosed psychiatric or learning disorders.

Research procedures were approved by the relevant Institutional Review Board. Adult participants provided written consent prior to participating in the study. Children and adolescents provided written assent, and their parents or guardians provided written consent on their behalf, prior to their participation in the study. All participants were compensated $60 for the experimental session. Participants were told that they would receive an additional bonus payment that would be based on their performance in the task; in reality, all participants received an additional $5 bonus payment.

Experimental task

Participants completed two blocks of four experimental tasks while undergoing functional magnetic resonance imaging (fMRI) (Figure 1). All tasks were framed within a single narrative.

Participants were told that they had a large collection of different postcards that they needed to stamp. In the first, frequency-learning task, participants viewed each of their 24 types of postcards, one by one. Critically, half of the postcards were displayed only once, while others repeated five times, such that participants completed 72 trials in total. Participants were instructed to press one of two buttons to indi-

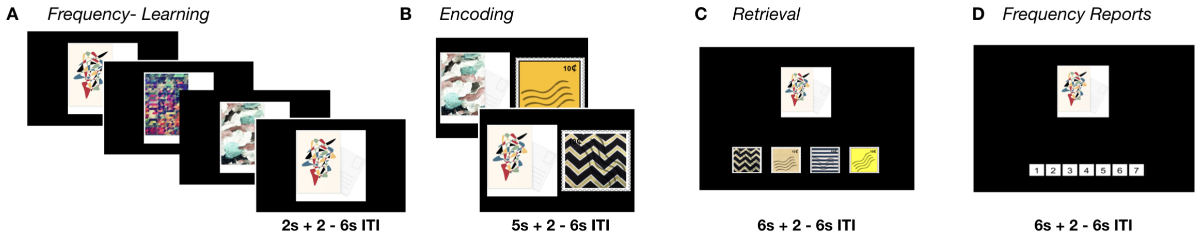

Figure 1: Participants completed four tasks while undergoing fMRI. Participants first learned the frequencies of each item (A) by viewing them one-by-one. They then were shown the information associated with each item (B). In the memory test, participants had to select the information associated with each item (C) and the item's original frequency (D).

cate whether the postcard was new or repeated. Further, they were told to try to remember how many of each item they had, as this would be useful for them later.

In the encoding task, participants saw each of their 24 types of postcards with their accompanying stamps. Participants were told that they would later have to stamp *all* of their postcards, earning one point for each postcard stamped correctly. Participants were further instructed that this meant that if they remembered the stamp that went on a type of postcard that they had five of, they could earn up to five points. Importantly, participants saw each postcard-stamp pair once, regardless of the postcard's original frequency.

Next, participants completed the retrieval task in which they saw each type of postcard and had to select the correct stamp from an array that included the correct stamp, a foil that was presented with a low-frequency postcard, a foil that was presented with a high-frequency postcard, and a novel foil. In the first part of the retrieval task, participants only responded to each item once. In other words, even if they had five of a particular postcard, they only selected the correct stamp for it *once*, such that participants completed an equal number of retrieval trials involving high-frequency and low-frequency items.

After retrieving the paired associates, participants were asked to explicitly report the number of each type of postcard they had, by thinking back to the very first frequency-learning task they completed. Participants pressed buttons that corresponded to the numbers 1 - 7 to make their responses.

Finally, participants completed a second round of the retrieval task in which they selected the stamp for each of the postcards they had five of four more times. Critically, while participants remained in the scanner, we did not collect fMRI data during this part of the task, nor did we analyze participants' behavioral responses. The purpose of including this second retrieval task was to maintain the task structure required for our value manipulation while simultaneously ensuring that each retrieval trial was only worth one point. In other words, if participants remembered the stamp that went on a postcard they had five of, including this part of the task meant that they *actually* had five opportunities to use that knowledge and select the correct stamp, earning one point each time they did so, up to a total of five points per high-frequency postcard. At the end of the retrieval task, participants saw how many total postcards they had stamped correctly across both parts of the retrieval task. Thus, in total, participants completed 72 retrieval trials and could earn up to 72 points: the first 24 trials included the 12 unique high-frequency postcards and the 12 unique low-frequency postcards, in a randomized order. This part of the retrieval test occurred *prior* to the explicit frequency reports, and data from this part of the experiment is included in both our behavioral and neural analyses. The latter 48 retrieval trials occurred *after* the explicit frequency reports, and included four more repetitions of each of the 12 unique high-frequency postcards, in a random order. Data from this part of the experiment was not analyzed, but participants were told that their performance on this part of the task influenced their bonus payments.

After completing all five parts of the task, participants completed a second block of all tasks with different stimuli (pictures and picture frames). The order of the blocks was counterbalanced across participants, such that half of them completed the block with picture and picture frames first.

All participants also completed the matrix reasoning and vocabulary portions of the Wechsler Abbreviated Scale of Intelligence (WASI-II), from which we derived IQ scores (Wechsler, 2011).

Behavioral analyses

All analyses were conducted in R. Mixed-effects models were implemented through the ”afex” package (Singmann et al., 2016). All models included random intercepts for each participant and item, and random slopes across all fixed effects and their interactions. For logistic models, significance of the fixed effects was tested with likelihood ratio tests. For linear models, significance of the fixed effects was tested with F tests with Kenward-Rogers approximations for degrees of freedom. In all analyses, age was included as a continuous variable. A linear regression revealed a significant negative relation between age and IQ, $F(1,88) = 5.29, p = .023$. To control for the influence of IQ, we included it as an interacting fixed effect in all behavioral analyses. To increase the power of our neuroimaging analyses, all analyses were collapsed across the two experimental blocks.

FMRI data acquisition, processing and analysis

Participants were scanned using a 3 Tesla Siemens Prisma scanner for approximately 1 hour. Prior to the day of the scan, children and adolescents completed a short mock scanning session to acclimate to the scanning environment and practice remaining still. On the day of the scan, all participants completed a 10-minute tutorial in which they practiced shortened versions of each phase of the task outside of the scanner.

Prior to the functional runs, high-resolution T1- and T2-weighted anatomical images were collected. Functional data were acquired with a T2*-weighted multi-echo EPI sequence (TR=2s, TEs=12.2, 29.48, 46.76, 64.04ms; MB factor = 2; 44 axial slices; 75° flip angle, 3-mm isotropic voxels). Data were preprocessed using fMRIPrep (Esteban et al., 2018, 2017), a robust preprocessing pipeline that adjusts to create the optimal workflow for the dataset, and visually inspected. Runs in which more than 15% of TRs were censored for motion (relative motion $>$ .9 mm framewise displacement) were excluded from neuroimaging analyses. Participants who did not have at least one usable run of each task (frequency-learning, encoding, retrieval, frequency reports) were excluded from all behavioral and neuroimaging analyses. Of the ninety participants included in the final data set, eight contributed only one run to encoding, and nine contributed only one run to retrieval.

All subsequent neuroimaging analyses were completed in FSL 6.0 (Jenkinson et al., 2012). Preprocessed BOLD data, registered to fMRIPrep's MNI152 template space and smoothed with a 5mm Gaussian kernel, were submitted to a GLM analyses to estimate relevant task effects. For both encoding and retrieval analyses, the model regressors included temporal onsets for high- and low-frequency trials, convolved with a double gamma hemodynamic response function. Nuisance regressors included 6-parameter motion correction values and their derivatives, framewise displacement values, censored frames, the first 6 anatomical noise components (aCompCor) from fMRIPrep, and cosine regressors from fMRIPrep to perform high-pass filtering of the data. Analyses were thresholded using a whole-brain correction of $z > 3.1$ and a cluster defining threshold of $p < .05$ using FLAME 1.

Results

Age-related change in frequency learning

First, we examined whether participants across our age range learned the frequency of items in their environments. In the frequency-learning task, participants' responses were both more accurate ($\chi^2(1) = 116.71, p < .0001$). and faster ($F(1,64.53) = 301.59, p < .0001$) as the number of repetitions of each item increased. Response accuracy increased with increasing age ($\chi^2(1) = 42.23, p < .0001$), while reaction times decreased ($F(1,87.35) = 21.77, p < .0001$). Despite the age-related improvements in task performance, participants across our entire age range were able to accurately identify the repeated images (Mean Accuracy: Children = .88, Adolescents = .92, Adults = .95).

Next, we asked whether there were any age-related differences in participants' abilities to transform their experiences of encountering each item into explicit representations of item frequencies. We computed frequency report error magnitude for each item by taking the absolute value of the difference between the participant's frequency report (1 - 7) and the true frequency (1 or 5). We then examined how these error magnitudes varied as a function true item frequency and age. While frequency report error magnitudes did not vary as a function of true item frequency ($p = .99$), they decreased with age, ($F(1,94.28) = 17.57, p < .0001$), particularly from childhood to adolescence (Mean error magnitudes: Children: 1.48; Adolescents: 1.10; Adults: 1.13; Figure 2). Thus older participants' explicit beliefs about item frequency more closely matched the statistics of their experienced environments.

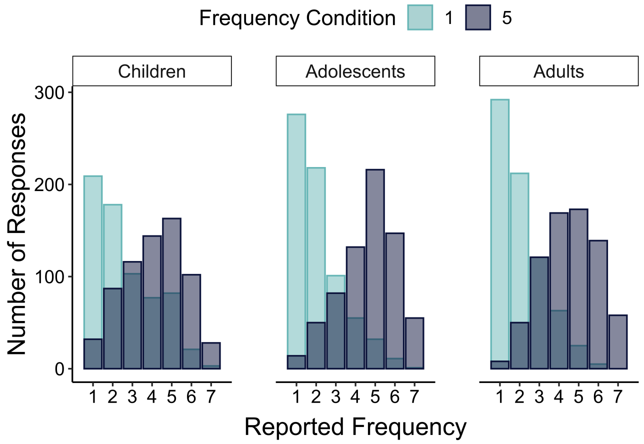

Figure 2: In their explicit reports, children, adolescents, and adults successfully differentiated items that had appeared once from items that had appeared five times. However, participants' explicit frequency reports became more accurate with increasing age.

Age-related change in memory prioritization

To address our primary behavioral question, we examined how item frequency influenced memory for associated information. Retrieval trials were coded as ”accurate” if participants selected the correct paired associate for the presented item from the array of four choices. As such, chance-level performance on the memory test was 25%.

We found that participants demonstrated higher memory accuracy for information associated with items in the high- relative to low-frequency condition, $\chi^2(1) = 16.78, p < .0001$. In addition, overall memory accuracy improved with increasing age, $\chi^2(1) = 34.31, p < .0001$. Critically, we observed an age x frequency condition interaction, such that older participants demonstrated a greater modulation of memory accuracy by frequency condition, $\chi^2(1) = 4.94, p = .03$ (Figure 3). In other words, with increasing age, individuals demonstrated increased prioritization of high-value information in memory.

We also examined how age, memory accuracy, and frequency condition influenced participants' response times at retrieval. Participants made faster responses on trials in which they responded accurately, $F(1, 76.55) = 61.94, p < .0001$. However, this effect was qualified by an age x memory accuracy interaction, such that memory accuracy decreased reaction times to a greater degree in older participants, $F(1, 90.36) = 32.09, p < .0001$. We further observed a memory accuracy x frequency condition interaction ($F(1, 3535.26) = 16.37, p < .0001$) such that on accurate trials, responses to items in the high-frequency condition tended to be faster than those in the low-frequency condition. Participants' sensitivity to frequency condition at retrieval suggests that learned value representations persisted beyond the initial encoding of associations, and may have influenced retrieval processes as well.

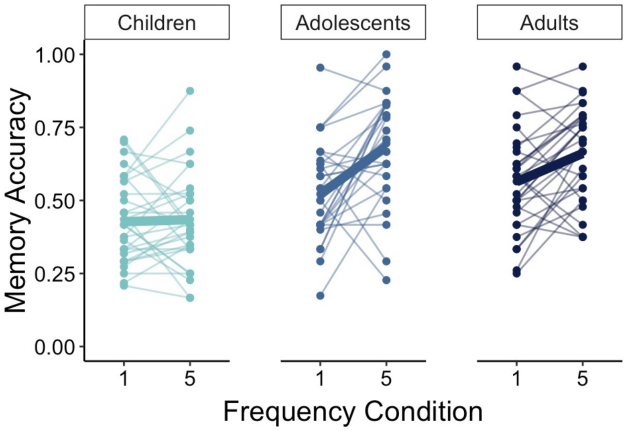

Figure 3: With increasing age, participants demonstrated increased value-based modulation of memory, as indicated by higher memory accuracy for information associated with items in the 5- relative to the 1-frequency condition. Thin lines indicate individual participant performance, while the thicker lines indicate age-group averages. Chance-level performance was 25%.

Neural mechanisms supporting value-guided memory

We next examined whether individuals recruited different neural circuitry while encoding pairs involving high- vs. low-frequency items. A whole-brain contrast revealed increased engagement of the right lPFC (1603 voxels at $x = -39$, $y = 18$, $z = 30$) and bilateral caudate (332 voxels at $x = -15$, $y = 6$, $z = 18$; 53 voxels at $x = 12$, $y = 12$, $z = 3$) during encoding of pairs involving high-frequency items (Figure 4). We further tested how both age and memory performance influenced neural activity during encoding. We repeated the high- vs. low-frequency contrast with different covariates: age and a memory difference score, computed for each participant by subtracting their mean memory accuracy in the low-frequency condition from their mean memory accuracy in the high-frequency condition. We did not detect age-related change in functional recruitment for encoding of pairs involving high- vs. low-frequency. However, memory difference scores were associated with greater modulation of right lPFC activity (201 voxels at $x = -48$, $y = 21$, $z = 27$). Participants who demonstrated the greatest degree of value-based memory modulation also demonstrated increased recruitment of the lPFC in the high- vs. low-frequency condition at encoding.

Finally, we examined the persistence of differential neural responses to high- vs. low-frequency items by examining neural activity during retrieval. Mirroring our encoding results, a whole-brain contrast revealed greater activity in the right lPFC (86 voxels at $x = -30$, $y = 3$, $z = 57$) and bilateral caudate (141 voxels at $x = 15$, $y = 0$, $z = 15$) during retrieval of the information associated with high- vs. low-frequency items. At retrieval, we did not detect modulation of functional recruitment of neural activity by age or memory difference scores.

Discussion

Using a recently developed task, we replicated our previous behavioral findings by demonstrating that from childhood to adulthood, individuals improved in their ability to extract signals of information value from their past experiences and use them to strategically modulate memory. Specifically, we found that children, adolescents, and adults, could track the repetitions of items in their environments. By adolescence, individuals could use their prior learning of item frequency to prioritize memory for information associated with high-frequency items, which ultimately enabled them to earn more reward.

Here, we extended our previous work by examining the neural mechanisms that support the recognition and use of information value to guide memory across development. We found that across our age range, the presentation of high-value information at encoding engaged striatal and prefrontal regions, including the caudate and lateral PFC, as we had hypothesized. Previous work has demonstrated that the caudate shares connections with the frontal cortex, including the lateral PFC, which may implement cognitive control processes (Miller & Cohen, 2001). One limitation of our design is that we were unable to examine the specific control processes that participants implemented to prioritize memory — they may have increased their mental rehearsal of high-value pairs, assigned them verbal labels, or tried to integrate them into preexisting associations in memory (e.g., "the sky-colored postcard goes with the sun-colored stamp.") Regardless of the specific strategy that participants used to encode the novel associations, interactions between the caudate and lPFC may

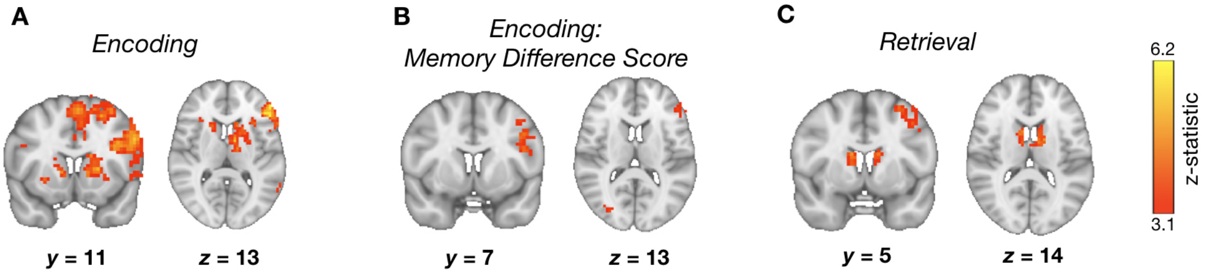

Figure 4: Participants demonstrated increased recruitment of the right lPFC and the bilateral caudate when presented with pairs involving high-frequency items at both encoding (A) and retrieval (C). Participants who showed the greatest difference in memory performance between the high- and low-frequency conditions also showed the greatest difference in right lPFC engagement between the high- and low-frequency condition at encoding (B).

have gated its implementation, supporting its upregulation during the presentation of high- relative to low-value information at encoding.

The differential recruitment of neural circuitry during encoding of associations with high- vs. low-frequency items was related to the extent to which participants successfully prioritized memory for high-value information. Specifically, participants who showed the greatest difference in memory accuracy for associations involving high- relative to low-frequency items also showed the greatest increase in right lPFC activity during presentation of pairs with high- vs. low-frequency items at encoding. This suggests that across people, the *recognition* of information value, which we expected to be reflected in reward responsive regions, may have been more consistent, while the *use* of information value to influence encoding varied to a greater extent and was a stronger predictor of value-based memory modulation.

Contrary to our initial hypothesis, we did not observe any modulation of our high- vs. low-value encoding contrast by age, despite our behavioral results showing age-related improvements in memory selectivity. Our whole-brain contrast may have been underpowered to detect age effects. Further, we observed heterogeneity in memory selectivity across age groups, such that some young participants demonstrated large effects of information value on memory and some older participants demonstrated small effects or no effect of information value on memory. The heterogeneity in performance across participants of similar ages may be why we observed a relation between neural activity and our memory difference score — which is a more direct readout of the magnitude of value-based memory modulation — but not between neural activity and age. It may also be the case that though participants across our age range showed similar levels of striatal and prefrontal activity during encoding, the computations implemented by these regions may have changed from childhood to adulthood. Children may have been equally likely to increase their engagement of strategic control processes when pairs involving high-frequency items were presented, but if the actual mnemonic strategies they attempted to implement were ill-suited to the task at hand, then this increase in strategic engagement would not be reflected in better memory performance.

Also contrary to our hypothesis, we did not observe any difference in MTL activity during the presentation of high- relative to low-value information at encoding. This may be because unlike tasks that have been used in past studies of motivated memory, our task required the retrieval of learned value signals during encoding of pairs with both low- and high-frequency items. One of the key features of our design was that rather than being presented with explicit value cues, participants had to consider all of their past experiences with the presented stimuli to determine the relative value of encoding associated information. Thus *all* items presented at encoding likely triggered the engagement of neural regions in the MTL involved in retrieving past experiences (Squire, 1992). The need for retrieval across encoding conditions may explain why we did not observe robust differences in MTL activation across conditions.

Finally, we observed increased engagement of the caudate and right lPFC during retrieval of high- relative to low-value information in the retrieval block itself. This suggests that we cannot rule out the possibility that differences in retrieval processes also contributed to participants' increased memory accuracy in the high- relative to the low-frequency condition. We designed our task such that encoding information associated with high-frequency items would yield more reward, whereas retrieving each association would always yield one point — participants could earn more points by remembering the high-frequency associations because they had more opportunities to retrieve them. Nevertheless, our retrieval response times and our neural data suggest that participants may have engaged different processes to retrieve more valuable associations. This finding is in line with prior work that has shown striatal involvement in value-based modulation of memory *retrieval* (Scimeca & Badre, 2012). As at encoding, the recognition of the value of a particular association may elicit the engagement of cognitive control mechanisms that increase the probability of successful retrieval (Scimeca

& Badre, 2012). Further work is needed to determine the extent to which developmental change in encoding vs. retrieval contribute to improvements in value-guided memory from childhood to adulthood.

Our findings demonstrate that from childhood to adulthood, individuals recruit a diverse network of neural circuitry to promote memory prioritization for high-value information, including the caudate and lateral PFC. Individual differences in memory prioritization were reflected in differential involvement of the lateral PFC during encoding, which suggests that the strategic *use* of item value to modulate encoding may be a greater source of variability in memory selectivity relative to the *recognition* of item value. Importantly, we also replicated our prior behavioral findings that demonstrated that individuals could learn the value of information through experience, and modulate memory based on *retrieved* value signals that were not explicitly presented at the time of encoding — a process that, relative to previous studies of motivated memory, may more closely mimic the memory challenges individuals face in real-world environments.

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